Mating strategies in primates: A game theoretical approach to infanticide

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Abstract: Infanticide by newly immigrated or newly dominant males is reported among a variety of taxa, such as birds, rodents, carnivores and primates. Here we present a game theoretical model to explain the presence and prevalence of infanticide in primate groups. We have formulated a three-player game involving two males and one female and show that the strategies of infanticide on the males' part and polyandrous mating on the females' part emerge as Nash equilibria that are stable under certain conditions. Moreover, we have identified all the Nash equilibria of the game and arranged them in a novel hierarchical scheme. Only in the subspace spanned by the males are the Nash equilibria found to be strict, and hence evolutionarily stable. We have therefore proposed a selection mechanism informed by adaptive dynamics to permit the females to transition to, and remain in, optimal equilibria after successive generations. Our model concludes that polyandrous mating by females is an optimal strategy for the females that minimizes infanticide and that infanticide confers advantage to the males only in certain regions of parameter space. We have shown that infanticide occurs during turbulent changes accompanying male immigration into the group. For changes in the dominance hierarchy within the group, we have shown that infanticide occurs only in primate groups where the chance for the killer to sire the next infant is high. These conclusions are confirmed by observations in the wild. This model thus has enabled us to pinpoint the fundamental processes behind the reproductive decisions of the players involved, which was not possible using earlier theoretical studies.

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Mating strategies in primates: A game theoretical approach to infanticide

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Abstract

Infanticide by newly immigrated or newly dominant males is reported among a variety of taxa, such as birds, rodents, carnivores and primates. Here we present a game theoretical model to explain the presence and prevalence of infanticide in primate groups. We have formulated a three-player game involving two males and one female and show that the strategies of infanticide on the males' part and polyandrous mating on the females' part emerge as Nash equilibria that are stable under certain conditions. Moreover, we have identified all the Nash equilibria of the game and arranged them in a novel hierarchical scheme. Only in the subspace spanned by the males are the Nash equilibria found to be strict, and hence evolutionarily stable. We have therefore proposed a selection mechanism informed by adaptive dynamics to permit the females to transition to, and remain in, optimal equilibria after successive generations. Our model concludes that polyandrous mating by females is an optimal strategy for the females that minimizes infanticide and that infanticide confers advantage to the males only in certain regions of parameter space. We have shown that infanticide occurs during turbulent changes

accompanying male immigration into the group. For changes in the dominance hierarchy within the group, we have shown that infanticide occurs only in primate groups where the chance for the killer to sire the next infant is high. These conclusions are confirmed by observations in the wild. This model thus has enabled us to pinpoint the fundamental processes behind the reproductive decisions of the players involved, which was not possible using earlier theoretical studies.

Keywords: Sexual selection, Infanticide, Polyandry, Reproductive strategies, Game Theory

1. Introduction

In a variety of mammals such as primates, carnivores and rodents, newly immigrated or newly dominant males are known to attack and kill dependent infants [1, 2, 3]. Hrdy [4] was the first to suggest that this unusual behavior was the product of sexual selection: by killing infants they had not sired, males advanced the timing of the mother's next estrus, and due to their new social position would have a high probability of siring this female's next infant. Infanticide would therefore be one of the most dramatic expressions of inter-sexual conflict [5, 6]. This is particularly true for primates with slow life history and the propensity to resume cycling when dependent infants are lost. These conditions provide ideal circumstances for reproductive gains, thereby making infanticide an adaptive strategy for the male but extremely costly for the female, who has a substantial investment in the form of lactation and gestation [7]. Indeed, among primates this phenomenon is remarkably common: It is reported in more than 40 species and may account for up to 25% of infant deaths [1, 5, 8, 9]. Although both the phenomenon and its interpretation have been questioned by some ([10, 11]; but see [12]), this hypothesis provides a far better fit with the observations on primates than any other alternatives [7]. Moreover, strong

empirical data supporting the infanticide hypothesis have been found in recent years [3, 13], including studies that determined paternities [14, 15]. Since infanticide almost always follows usurpation or incapacitation of the former dominant male, who is the likely sire, it is clear that male protection plays an important role in infant survival [7]. Thus, considering the costs involved, infanticide is expected to have driven selection on counterstrategies by both the mother and the likely sire from the point of view of reduction in infanticide [9, 12, 16, 17, 18].

Since infanticide is inherently adaptive for the males and at the same time, extremely costly for the female it is important to study its impact formally on the overall reproductive behavior of primate males and females. Our earlier mathematical models are based on a phenomenological approach. We have demonstrated the existence of a basic conflict of interest between the dominant male and the female and also between the dominant and other competing males [18, 19, 20]. We have derived conditions under which infanticide is adaptive and its resulting impact on social composition of primate groups. Furthermore, one of our models has shown that despite having a conflict with the subordinate male and/or the rivals, occasionally, the dominant male earns a higher payoff by conceding some paternity to other males; this prediction has been supported with empirical data on baboons [21] (See also [22]).

It would be of interest to know the fundamental processes behind male-female reproductive decisions in this social situation of conflict and cooperation and we thus propose a framework that will complement our earlier theoretical investigations [18, 19]. We propose that, starting from first principles and with a minimum number of assumptions, it can be best approached by using the mathematical theory of games because there is involvement of multiple players and the reproductive decisions made by each player has an impact on the fitness of every player involved. In this framework, every player chooses its strategies from a fixed set and then

rather than searching for a globally optimal outcome, we look for combinations of strategies, where each player's strategy gives the best outcome to that player based on the others' strategies. Such combinations are known as Nash equilibria. Furthermore, we need to determine the stability of these strategy equilibria against competing strategies.

Our model differs from that of Broom et al [23] in that we also consider the options of the female and of both insider and immigrant males. It is similar to other social strategy games on deforestation (e.g. See [24]) or on decision-making in political systems and large organizations [25]. In this paper, we will demonstrate that the reproductive decisions made by males and females are in Nash Equilibria, and that only small regions of parameter space lead to stable Nash Equilibria that admit infanticide which, for the first time, will also produce a theoretical explanation for the adaptive but rare nature of infanticide on the whole.

2. Model

We develop a game theory model that describes the mating strategies of females and attitudes towards infants by males in primate groups. Standard Game Theory assumes a finite number of players and a finite number of strategies for each player. Although many primate groups contain numerous potential players, we limit the game to a two-male, one-female system. This game involves one female because in species with estrous asynchrony, female mating decisions are largely independent of each other (e.g. [26]). The two-male approximation is justified because most of the male-male interactions are dyadic (unless coalitions among males are present [27]). A male's dominance is based on his strength relative to the other (σ). The species modeled here are iteroparous and hence females give birth multiple times in a lifetime, up to a dozen times for some species [28].

In constructing our model, we assign a set of pure strategies to each player. Both males possess the same set of pure strategies, viz. "attack (A)," "defend (D)," and "show indifference toward (I)" the offspring. The female's pure strategies are to mate solely with male 1 (M1) and mate solely with male 2 (M2). Each player may also utilize a mixed strategy, with different weights attached to their pure strategies. A strategy profile is denoted by an ordered *n*-tuple of individual strategies. For example, a pure strategy profile could be S = (A,D,M1). A mixed strategy is denoted as $M=(X_{A,D},X_I,X_{M1})$, where the subscripts are the supporting pure strategies. In the previous example, male 1 is playing a strategy with non-zero weights attached to his attack and defend strategies, male 2, strictly the ignore strategy, and the female, strictly "mate with male 1" (see [29]).

The physical interpretation of a mixed strategy in game theory has been contested in recent decades [30, 31]. In the female's case, the interpretation is straightforward. Each weight to her pure strategy represents the proportion of matings with that particular male among all her matings with both males within one turn of the game, i.e. one full birth interval. Thus, if she is playing a mixed strategy with 0.3 weight assigned to her M1 (denoted in our game by the variable p) pure strategy and 0.7 weight assigned to her M2 pure strategy, out of all her total matings with males 1 and 2, 30% of them are with male 1 and 70% with male 2.

For the males, various interpretations of their mixed strategies can be put forward. For this game, we chose the multiple-action interpretation, in which the males have multiple opportunities to act against the infant, and their pure strategy weights represent the percentage of times they take that action at every opportunity. However, in this interpretation, the number of opportunities *n* a male has is ambiguous: it is assumed to be a finite number, dependent on external factors, but is not necessarily constant, because if the infant is successfully killed early

on, n could be smaller. Also, the order in which a male takes his actions is undefined. It is unclear how these two features of the multiple-action interpretation affect the outcome of this model. Regardless, the model treats these multiple actions as if they are equivalent to a single action.

Apart from the strategies, the model relies on five external parameters that depend on environmental factors such as group composition, duration of male tenure, length of gestation and lactation periods, life history, and the physiological conditions of the males. The values of these parameters range between 0 and 1, exclusive. The parameter μ is the probability of a male siring a subsequent offspring with the female after committing infanticide (where 1-μ is the corresponding chance of the other male siring the next offspring), σ is the normalized relative strength of the males (corresponding to the likelihood that male 1 wins a conflict with male 2), c is the normalized cost, weighted by σ, to a male while defending an offspring attacked by another male. In the model, there is no cost to an attacking male because it is assumed that attacks are always opportunistic, that is, at a time favorable to the attacker. Since the attacker has the choice of the timing and conditions of the attack, costs for an attack are negligible compared to the cost of defense. The cost of defense is always assumed to be less than 1, even though defense might incur losses of future potential infants, because the game only considers the presence or absence of one infant for the male at the end of the turn, and does not take into account future game turns. The parameter l is a "lookout" cost borne when a male defends an infant not immediately threatened, and k is the normalized reproductive cost to the female, in either time or energy, from the loss of the initial infant. Table 1 gives concise descriptions of these parameters. The probabilistic interpretation of external parameters is founded on the possible existence of ensembles of primate groups, i.e. given multiple simultaneous instances of the game by any

group of players. Thus, the parameters may be interpreted as the expected value of that parameter over those instances.

The payoff for each player is the number of offspring sired at the end of the turn minus the costs imposed upon the player. Since our payoff tables are three-dimensional, Tables 2-4 represent them as a pair of two-dimensional tables, one for each of the female's pure strategies.

One turn in the game corresponds to a period of one inter-birth interval for the female. The turn ends either with the weaning of the initial offspring or the birth of a second offspring in the event of infanticide. These events do not systematically affect the real-time duration of each turn provided the infants are killed approximately one gestation period before weaning. This assumption is not unreasonable [7]. Thus a game turn always ends with one offspring present, and the essence of the game is determining how much fitness each player gains when external parameters are considered.

As shown in Table 4, the expected payoffs for the female's two pure strategies are identical. This reflects the fact that in non-cooperative game theory, a best response is chosen after fixing the other players' strategies. In essence, the female's choice within the game has no effect on her payoff, because at this point the males have already chosen their strategy, and a change of her strategy cannot deter them.

A standard approach, after identification of players and strategies, in development of game theoretic models involves two steps: i). Construct a payoff table based on pure strategies, and ii). Solve the payoff equations and determine Nash Equilibria (NEs). In this case, because the NEs are not strict, we need to analyze the stability and growth of these equilibria within a population over multiple instances of the game.

3. Results

The model generates several NEs under different values of the external parameters. We classified the equilibria here based on the total number of supports (See [29]). The existence of each equilibrium relies on relations between external parameters and strategy weights. Some of these relations may involve equalities, which generate subspaces of measure zero, such as points, lines, or surfaces of the parameter space. Since the external parameters can only be measured with limited accuracy, fulfillment of equality conditions will be difficult to assess. For these reasons, we will not discuss these non-generic cases.

The NE and their conditions are listed in Table 5. Note that the equilibria listed in the table can be partitioned into two categories, passive and aggressive. In passive profiles, neither male attacks, whereas in aggressive profiles, at least one male attacks.

A rather surprising NE among aggressive profiles is where both males attack the infant. This result arises if the rewards for killing the infant outweigh the potential for paternity and cost of defense for both males. Certain values of the external parameters may induce a male to kill an infant that is almost certainly his, a mathematical possibility that is unlikely to be realized (see discussion).

Based on the analysis of these equilibria, the key results of the model can now be elucidated. First, in all the profiles, the males play only pure strategies. Consequently, on the subspace spanned by all the male players, all these equilibria are strict.

Second, the female's payoff in the aggressive profiles is always lower than her payoff in the passive profile (Figure 1). The passive profile is permissible only under the conditions $p \geq \mu$ and $1\text{-}p \geq \mu$, where p is the female's mixed strategy weight for her pure strategy M1. Thus the female's payoff is maximized if p is between μ and $1\text{-}\mu$. Thus, for a passive profile to be a NE, μ

must be less than or equal to 0.5. This suggests that for the female, the best strategies involve distributing paternity as evenly as possible between the two males. For high μ [i.e, $\mu > 0.5$] the passive profile is no longer a NE, and instead aggressive profiles are NEs. The female's maximum payoff is then dependent on σ, and is achieved by biasing paternity towards the stronger male to achieve the (A,D) or (D,A) profiles (Figure 1).

Standard game theory cannot specify how the female attains her optimal equilibria. Because all of the female's responses are best responses to any strategy profile, the female has no incentive within the game-theoretical framework to deviate from any strategy she is currently playing. This means that so long as the males' strategies are fixed, her payoff does not depend on her strategy. Moreover, the game makes no provision on whether the female would stay at a strategy that is optimal. A framework called "adaptive dynamics" [32] allows considerations of transitions to Nash equilibria, and we discuss the details of this issue in the discussion.

If we consider all three players, none of the NEs are strict and hence cannot be evolutionarily stable. However, NEs evaluated on the subspace spanned by the males are strict, and hence are evolutionarily stable. Thus passive NEs are the evolutionarily stable strategies (ESS) for $\mu < 0.5$, and the aggressive NEs the ESS for $\mu > 0.5$. Hostile takeovers from outside males can be characterized within this model as $p = 0$ when male 1 is the outsider. Under this condition, passive NEs vanish. Male 1 (the outsider) will always attack and male 2 will either defend or ignore, depending on the relative strength of the males and the cost of defense.

4. Discussion

As discussed in the results section, the key results of our model state that 1) males play only pure strategies in all viable NEs, and hence the NE on the parameter subspace spanned by

the males is strict; and 2) the female receives the highest payoffs in the passive profiles, which are attainable only if p is between the values μ and 1-μ. i.e., $\mu \leq 0.5$.

One aspect of the game that deserves attention is the timing of the players' actions. In standard game theory, the choice of a player's action in each turn is decided by the strategy profile played in the previous turn. All players choose their action for the next turn simultaneously, and the new strategy profile is generated. However, our game does not posit a simultaneous deciding of strategies by the players. Rather, the female chooses her strategy, and the males then simultaneously choose their strategies based on the female's current strategy. This is to suggest that the female distributes her paternity first, before all other actions occur. Once the infant is born, the males then choose their strategies, and the turn is played until the infant is weaned or killed. We believe the structure of the standard game is a sufficient approximation for our model.

Another potential issue of the model worth discussing is that it makes no mention of which of the NEs are stable, or how they are reached. Without further refinement, the problem of female choice remains: Within the game-theoretical framework, the female has no incentive for changing her strategy, since all her responses are best responses. Thus there is no pathway for the female to reach the passive profiles that maximize her payoff. However, transition between stable equilibria are generally identified by formulating the game as an evolutionary game. Evolutionary game theory utilizes the concepts of large player pools, mutations, and a selection process to analyze the stability of NEs. When viewed as an evolutionary game, however, the model fails to provide any stable equilibria by any of the accepted definitions, because none of the NEs generated are strict: a crucial requirement for stability. Even weaker variants of stability, such as Robustness against Equilibrium Entrants, give no insight (see [29]).

However, as shown above, NEs are stable on the subspace spanned by the males' strategies, and hence are ESS.

Since all of the female's responses are best responses, none of the resulting NEs can be strict. Hence, following adaptive dynamics, which allows for transitions between equilibria (see [29], [32]), we devise a selection mechanism that adjusts the value of p (the weight attached to the female mixed strategy M1). We expect that the game takes place multiple times within one primate group. Each female is paired with two males and chooses her value of p. After birth of the infant, the males then choose their strategies such that a Nash equilibrium is settled upon. At the end of the turn, each female receives a fitness payoff based on the Nash equilibrium that was reached during the game turn. As it happens, polyandrous females receive a higher payoff than the others. Our selection mechanism states that all female strategies receiving a higher than average payoff after each game turn will propagate throughout the population. Consequently, since the female strategies that lead to passive equilibria give the highest payoff, the females in the group will play those strategies more and more as the game progresses within a primate group.

This selection mechanism permits a transition to passive equilibria for the females, thus optimizing their payoff. As noted earlier, the passive profile requires that the female distributes paternity between the two males, promoting polyandrous mating and discouraging infanticide. This selection mechanism can gradually shift the value of p over all the females toward an optimal, fixed value, thus allowing us to treat it as a fixed external parameter for the males. If p is considered an external parameter, the male strategy profiles, since they are all pure, are evolutionarily stable within the subspace spanned by the males' strategies.

As stated earlier, given enough time and certain external parameters, all the strategy profiles within the population will become passive. This can only occur in populations where $\mu \leq 0.5$, i.e, where the biological and environmental conditions allow for female choice (see below).

Note that the parameter μ is independent of the parameter σ. This is to suggest that the chance of siring an infant after committing infanticide is not necessarily related to the strength of the male. Infanticide is an opportunistic action, meaning that the attacker may time his assault for an ideal moment, preferably when the mother and any defending males temporarily let down their guard.

In our model, μ is also independent of p, whereas in reality, there would probably be some correlation between the two. This correlation is assumed to be minimal, and so has been neglected. The parameter p represents the direct, explicit, choice of a female individual, whereas μ is an external parameter that represents evolutionary, indirect effects of paternity distribution, e.g. estrous synchrony, etc., and hence can only change slowly, especially through genetic change. It should be emphasized be that μ does not represent direct female choice. Like the males, the female only makes one "decision" per game turn. A different model could reflect the modest correlation between p and μ.

The value of μ will be driven by the reproductive biology and ecology of the species in question. The situation where $\mu \geq 0.5$ is the most common among sexually dimorphic species [33] because at $\mu < 0.5$, the male that commits infanticide actually has a smaller chance than the other male of siring the next infant. Indeed, the most common scenario that permits the *passive* NEs under these circumstances is with μ=0.5, where advantages in committing infanticide have been effectively neutralized. This value of μ constrains p, a behavioral component of female

choice, to be equal to 0.5, which the female achieves by turning the male mating competition into a complete scramble (e.g. bonobos; see [19]).

The most common context of infanticide in primates is when paternity of one male is assured (i.e. p=0 or 1) and aggressive male profiles are the only realizable profiles. This commonly occurs when there is a hostile takeover by an outside male, who has a zero probability of paternity.

It should be noted that some values of the external parameters in the game may never be physically realized. When the cost of defending an attacked infant is extremely high compared to the gain in fitness (i.e. c is close to one) and at the same time, the probability of siring the next infant by the killer is high, one may observe unphysical solutions of the game viz, a scenario where a father attacks his own infant. However, such extreme values of c and μ are not realistic. Usually, the cost of defense is expected to be a small fraction of the fitness payoff of siring an infant.

Indirect measurement of external parameters.

We believe that the model is testable because the expected values of the external parameters can indeed be measured to a certain degree of accuracy. The parameter c, which is defined as the expected cost of the male of defending an attacked infant over all the iterations, can be estimated by observing similar situations within various primate groups as if the same game is played multiple times. Similarly the relative strength σ of the male can be estimated by noting the proportion of fights won. Future paternity probability after infanticide μ is abstract and cannot be directly estimated, but would be close to the probability that the male achieves the

dominant position during a subsequent changeover. For the female, cost of child-rearing/bearing k would be something like the proportion of reproductive time lost during a reproductive period.

5. Conclusion

Our main goal in this paper was to formulate a general model based on a game-theoretical approach to explain any multiplayer social phenomenon where players have a choice among a finite number of actions. The present model complements the phenomenological model proposed by Pradhan & van Schaik [19] (also see [18]). Indeed, the game theoretical model not only explains female polyandry in primates, but also explains the fundamental processes responsible for reproductive decisions by both the males and the female. Moreover, we also show that the relevant stable equilibria are amenable only over a small regime of parameter space, thereby explaining for the first time why infanticide is rare in spite of being an adaptive male strategy. Thus, the game-theory approach has both confirmed and expanded the phenomenological approach.

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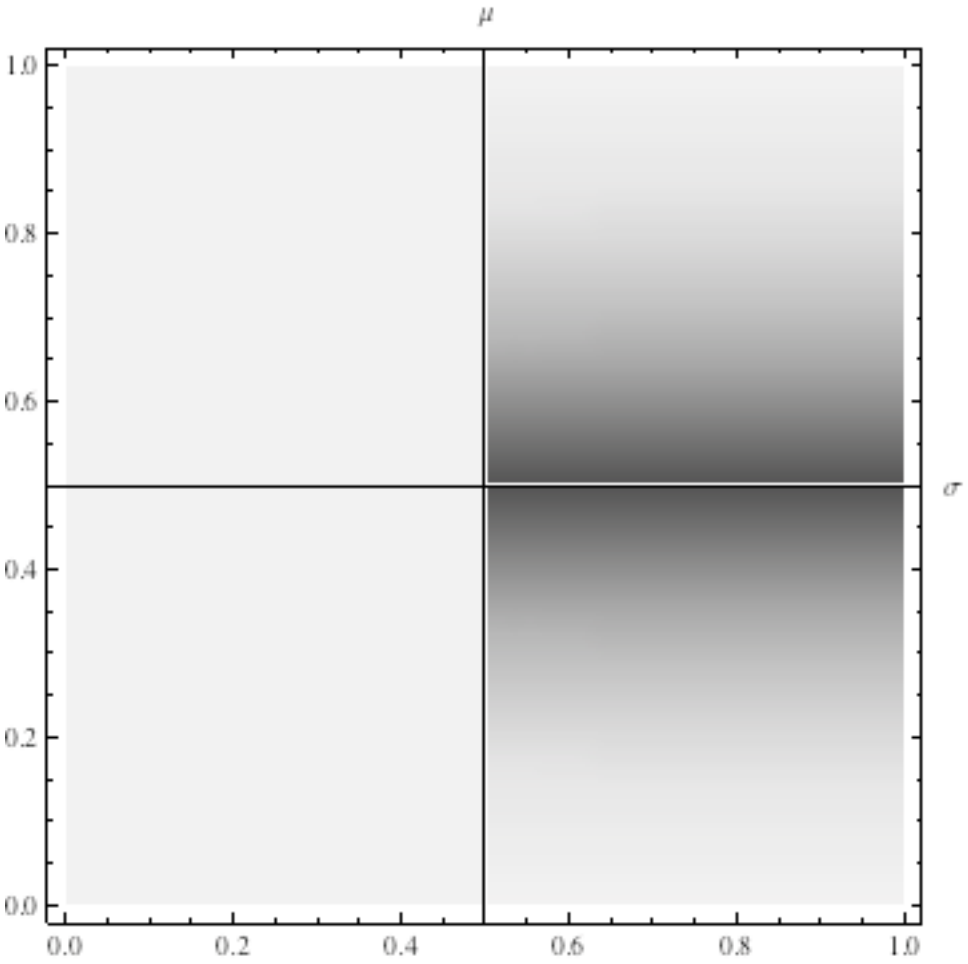
Figure Captions

Figure 1: Maximum female payoff for the NE profiles as a function of μ and σ

A lighter color represents a higher payoff. For $\mu \leq 0.5$, passive strategies prevail as long as the female chooses an appropriate value of p (see Table 5). For $\mu > 0.5$, the female maximizes her payoff by skewing p towards the strongest male (enough to elicit defense in the case of the stronger male).



List of Tables

Parameter	Description
μ	Probability for a male who commits infanticide to sire the next infant.
σ	Probability male one wins a fight against male two
c	Normalized expected cost of defending an attacked infant
l	"Lookout" expected cost for defending an infant not immediately threatened
k	Normalized reproductive cost to the female, in either time or energy, from the loss of the initial infant

Table 1: Description of the external parameters in the game.

(a)

Male 2 Male 1	A	D	I
Attack (A)	$\sigma\mu+(1-\sigma)(1-\mu)$	$\sigma\mu+(1-\sigma)$	μ
Defend (D)	$\sigma+(1-\sigma)(1-\mu)-(1-\sigma)c$	$1-l$	$1-l$
Ignore (I)	$1-\mu$	1	1

(b)

Male 2 Male 1	A	D	I
A	$\sigma\mu+(1-\sigma)(1-\mu)$	$\sigma\mu$	μ
D	$(1-\sigma)(1-\mu)-(1-\sigma)c$	$-l$	$-l$
I	$1-\mu$	0	0

Table 2: Payoff tables for Male 1 given that the female is following strategy M1 (a) or M2 (b) respectively. Parameters as defined in Table 1. As an example in calculating payoff cells, in the scenario where both males attack the infant, the payoff of Male 1 is the convex combination of the chance of siring an infant after losing the fight times the likelihood of losing and the chance of siring an infant after winning the fight times the likelihood of winning the fight. Therefore, we write the payoff as $0(1 - \mu)(1 - \sigma) + \mu\sigma$.

(a)

Male 1 Male 2	A	D	I
A	$(1-\sigma)\mu+\sigma(1-\mu)$	$(1-\sigma)\mu+\sigma$	μ
D	$(1-\sigma)+\sigma(1-\mu)-\sigma c$	$1-l$	$1-l$
I	$1-\mu$	1	1

(b)

Male 1 Male 2	A	D	I
A	$(1-\sigma)\mu+\sigma(1-\mu)$	$(1-\sigma)\mu$	μ
D	$\sigma(1-\mu)-\sigma c$	$-l$	$-l$
I	$1-\mu$	0	0

Table 3: Payoff tables for Male 2 given that the female is following strategy M2 (a) or M1 (b) respectively. Parameters as defined in Table 1. As an example in calculating payoff cells, If Male 1 attacks, Male 2 defends, and the female mates exclusively with Male 1, the payoff for Male 2 is the convex combination of his chance of successfully defending times the payoff of defending $(1-\sigma)0$, and the chance of unsuccessfully defending times the payoff of losing an infanticide fight $\sigma(1-\mu)$, minus the cost of defense σc. We can therefore write the payoff as $(1-\sigma)0+\sigma\mu-\sigma c$.

Male 2 Male 1	A	D	I
A	1-k	1-σk	1-k
D	1+σk-k	1	1
I	1-k	1	1

Table 4: Payoff table for the Female, where k is the reproductive cost of bearing an additional offspring for the female. Since the payoffs are identical regardless of the female's pure strategy, the three-dimensional payoff table can be condensed into a two-dimensional table. If the female loses the offspring (for example under the conditions (A,A), (A,I) or (I,A)), she bears the cost k for the new offspring.

Nash Equilibria	Number of Pure Strategies Used	Conditions
$(X_A,X_A,X_{M1,M2})$	4	$\mu \geq \max\{0.5, p\text{-}c(1\text{-}1/\sigma), ((1\text{-}p)(1\text{-}\sigma)\text{-}\sigma c)/(1\text{-}\sigma)\}$
$(X_A,X_D,X_{M1,M2})$	4	$(\sigma+\sigma c+p\text{-}1\text{-}p\sigma)/(\sigma\text{-}1) \geq \mu \geq \max\{p, (p\text{-}p\sigma+\sigma c)/(1\text{-}\sigma)\}$
$(X_D,X_A,X_{M1,M2})$	4	$(\text{-}c+c\sigma+p\sigma)/\sigma \geq \mu \geq \max\{1\text{-}p, (\text{-}p\sigma+\sigma\text{-}c\text{-}c\sigma)/\sigma,\}$
$(X_A,X_I,X_{M1,M2})$	4	$0.5 \geq \mu \geq \max\{p,(p\sigma\text{-}p\text{-}\sigma c)/(\sigma\text{-}1)\}$
$(X_I,X_A,X_{M1,M2})$	4	$\min\{1/2, (\text{-}p\sigma+\sigma+c\text{-}c\sigma)/\sigma\} \geq \mu \geq 1\text{-}p$
$(X_I,X_I,X_{M1,M2})$	4	$\mu \leq \min\{p,1\text{-}p\}$

Table 5: List of all Nash equilibria profiles whose conditions are exclusively inequalities, and the total number of pure strategies employed in each profile.

Appendices

A. Example: Finding Conditions for Nash Equilibria with varying number of supports for each player

Consider a strategy profile ($X_{D,I}$,$X_{D,I}$,$X_{M1,M2}$). In this scenario, Males 1 and 2 are permitted to randomize anywhere on the defend/ignore line of their strategy space, while the female may have any mixed strategy. Let us call a_1, d_1 , a_2, d_2, and p, the mixed strategy weights to male 1's A and D pure strategies, male 2's A and D pure strategies, and the female's M1 pure strategy, respectively. We look at the expected payoffs of each pure strategy to see what conditions need to be met for Defend and Ignore to be best responses for Males 1 and 2 (When u(D) and u(I) are equal and both larger than u(A), i.e. $u(I) = u(D) \geq u(A)$). Since neither of the males are attacking, we know a_1 and a_2 are both 0:

$u_1(A)=pd_2(\sigma\mu+(1-\sigma))+p(1-d_2)\mu+(1-p)d_2(\sigma\mu)+(1-p)(1-d_2)\mu$

$u_1(D)=pd_2(1-l)+ p(1-d_2)(1-l)+(1-p)d_2(-l)+(1-p)(1-d_2)(-l)=p-l$

$u_1(I)= pd_2(1)+ p(1-d_2)(1)+(1-p)d_2(0)+(1-p)(1-d_2)(0)=p$

$u_2(A)=(1-p)d_1((1-\sigma)\mu+\sigma)+(1-p)(1-d_1)\mu+pd_1((1-\sigma)\mu)+p(1-d_1)\mu$

$u_2(D)=(1-p)d_1(1-l)+(1-p)(1-d_1)(1-l)+ pd_2(-l)+p(1-d_2)(-l)= 1-p-l$

$u_2(I)=(1-p)d_1(1)+(1-p)(1-d_1)(1)+ pd_2(0)+p(1-d_2)(0)= 1-p$

Since p is always greater than p-l, randomization on the defend/ignore line is ruled out as a logical course of action for male 1. He would rather play ignore entirely than any amount of defend in this profile. The same argument can be made for male 2. Thus, this profile is not a NE.

B. Explanation of Cells in the Payoff Tables

(A,A,M1): Both males attack male 1's infant.

Male 1 has a σ chance of winning the fight to kill the infant, after which he kills his own infant and has gains μ from siring the next infant. He has a (1-σ) of losing the fight, in which case his payoff is (1-μ). Therefore, his payoff for this pure profile is σμ+(1-σ)(1-μ).

Male 2 has a (1-σ) chance of winning the fight, in which case he attains μ, and a σ chance of losing, in which he gets (1-μ). His final payoff is therefore (1-σ)μ+σ(1-μ).

Regardless of who wins and manages to kill the infant, the female receives a payoff of 1 (at least one infant is alive at the end of the game) minus the costs k for rearing an additional infant, for a total payoff of 1-k.

A similar analysis can be made for (A,A,M2), in which both males attack male 2's child.

(A,D,M1): Male 1 attacks his own infant, and male 2 defends male 1's infant.

Male 1 has a σ chance of winning the fight, in which case he receives μ from the next infant. He has a (1-σ) chance of losing the fight, in which case his infant remains alive and he receives a payoff of one. Therefore, his payoff for this pure profile is σμ+(1-σ).

Male 2 has a (1-σ) chance of winning the fight, in which he successfully defends male one's infant and therefore has a payoff of zero. He has a σ chance of losing, in which case he gets (1-μ). He also has a fixed cost for defense, -σc (the stronger male 1 is, the higher male 2's defense cost). Therefore, his payoff for this pure profile is $0(1-\sigma)+\sigma(1-\mu)-\sigma c=\sigma(1-\mu)-\sigma c$.

The female receives a payoff of one, because at least one infant is alive at the end of the game, minus the cost of rearing another infant if male 1 successfully kills the infant, for a total cost of 1-σk.

A similar analysis can be applied for the (D,A,M2) profile, where male 2 defends male 1's infant.

(D,A,M1): Male 1 defends his own infant, while male 2 attacks.

Male 1 has a σ chance of succesfully defending his infant, in which case he receives a payoff of 1. He has a (1-σ) chance of losing the fight, in which case he receives a payoff of (1-μ). He also has a fixed defense cost of (1-σ)c. Therefore, his final payoff for this profile is $\sigma+(1-\sigma)(1-\mu)-(1-\sigma)c$.

Male 2 has a (1-σ) chance of winning the fight, in which case he successfully kills the infant gets a payoff of μ. He has a σ chance of losing the fight, in which case male 1 successfully defends and male 2's payoff is 0. His payoff is therefore $\sigma+(1-\sigma)\mu=(1-\sigma)\mu$.

The female receives a payoff of 1, because at least one infant is alive at the end of the game, minus the costs k if male 2 successfully attacks and kills the infant, for a total payoff of $1-(1-\sigma)k$.

A similar analysis can be made for the (A,D,M2) profile, where male 1 attacks and male 2 defends male 2's child.

(D,D,M1): both males defend male 1's child.

Male 1 receives a payoff of 1-l, l being the lookout cost of defense. Male 2 receives a payoff of -l. The female receives a payoff of 1, since her initial child remains alive at the end of the game.

A similar analysis can be made for all the passive profiles (D,D,M2), (D,I,M1), (I,I,M1), etc.

(A,I,M1): Male 1 attacks his own child, while male 2 ignores.

Males 1 automatically kills his infant and receives a payoff of μ. Male two receives a corresponding payoff of $(1-\mu)$.

The female receives a payoff of 1-k, since her initial infant is always killed in these profiles.

A similar analysis can be made from (I,A,M2), (A,I,M2), and (I,A,M1).